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Feeding attributes of four species of Collembola in a pine forest soil

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With 3 figures

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1. Introduction

Collembola usually live in soil and litter and are a numerically abundant group among the soil arthropods. They may play an important role in soil formation and litter decomposition. An understanding of their feeding attributes is important in assessing their role in such biological processes in soil and comparative studies of feeding attributes among populations provides further useful information concerning the organization of the collembolan community.

The feeding biology of Collembola has been studied for field and laboratory populations. Laboratory studies have shown that most collembolan species feed on a wide variety of foods in soil, but show a clear preference among available foods (e.g. Dunger 1956, Visser & Whittaker 1977 and Addison & Parkinson 1978). In contrast, field populations usually show no food preferences as indicated by the examination of gut contents of animals collected in the field which consisted largely of the most abundant foods in soil such as decomposing plant matter and fungi (e.g. Poole 1957, Knight & Angel 1967, Bödvarsson 1970, and Gilmore & Raffensperger 1970). Anderson & Healey (1972) have related the low degree of food specialization of Collembola to an excess of food in the soil.

In this study area, 36 species of Collembola have been recorded. These can be divided into two ecologically related species groups, namely surface and humus dwelling species. In this study, we chose two surface dwelling species, *Isotoma carpenteri* Boerner and *Tomocerus varius* Folsom and two humus dwelling species, *Folsomia octoculata* Handschin and *Onychiurus decemsetosus* Yosii, as representatives of each life form group. The objectives of this study were to assess the seasonal changes in feeding activities and the feeding preferences of the four species of Collembola. These feeding attributes are discussed in connection with the community organization of the Collembola. This paper is part of series dealing with ecology of Collembola in a pine forest soil in Japan (Takeda 1973, 1976, 1978, 1979a & 1979b).

2. Study area and methods

The study was carried out in a pine forest located in Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of the centre of Kyoto City. Details of the study area are given in Takeda (1973, 1976). The boundary between the A and B soil layers is very distinct. The organic soil layers (A_0) consist of three zones, i.e. the L, F, and H layers. The L layer is about 1 cm in thickness, consisting of pine needles and other fallen leaves. The F layer is about 2—3 cm in thickness consisting of partially decomposed litter with portions of recognizable plant structures and rootlets. The H-A layer is only about 0.5 cm in thickness. The B layer is situated at 4—5 cm depth. The experimental station meterorological records were used in this study (Kyoto University Forest 1981). On each sampling occasion, soil temperature was measured with mercury in glass thermometers set at 4 cm in depth in the study plot. The water contents of soil were measured by taking soil samples and were expressed as the ratio of water to dry weight of soil. The records of soil temperature and water contents are shown in Fig. 1.

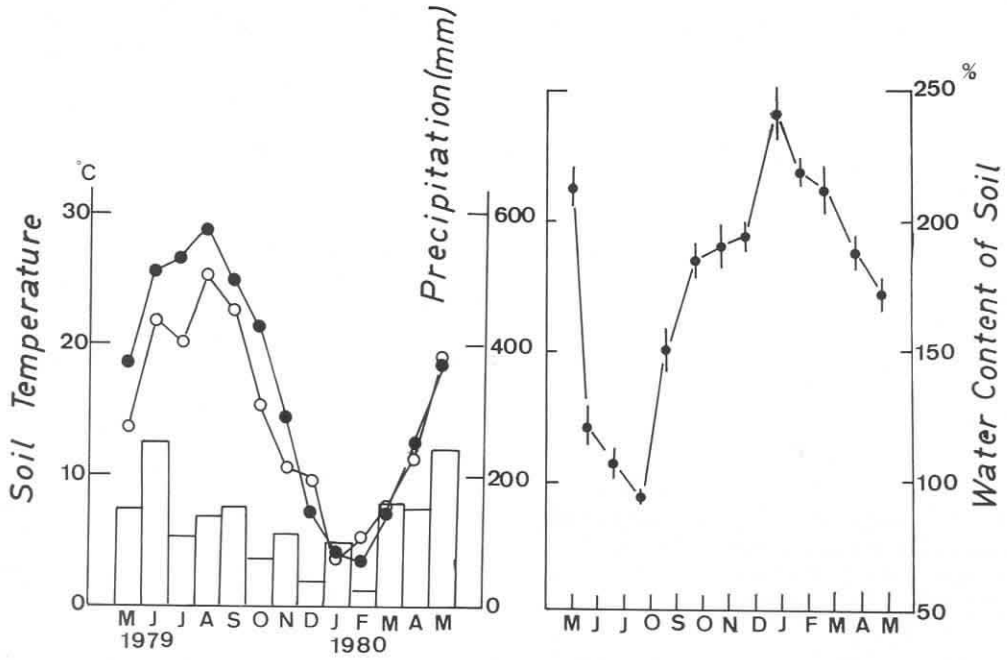

Fig. 1. Seasonal changes in air (●———●) and soil (○———○) temperature and precipitation during study period (left) and seasonal changes in soil water content at 0—5 cm depth (right; bars ndicate standard errors).

Sampling of soil animals was carried out at monthly intervals during the period from May 1979 to May 1980 in a plot of 10×10 m in area chosen in a pine forest. The sampling plot consisted of 20 sub-plots each of 5 m² in area. Soil cores each of 200 cm² in area and 4 cm in thickness were taken from the plot with a sharp knife. On each sampling date, 10 soil cores were taken from the 10 subiplots randomly chosen among the 20 sub-plots. In addition, two sets of 5 soil samples each of 200 cm² in area and 4 cm in depth were taken from the study plot on 15th October 1981 to compare the proportion of individuals with gut contents from a Tullgren extraction with those extracted by flotation. The soil samples for the flotation were placed in a beaker and a solution of sugar was poured into it to float collembolan individuals. The second set of samples were extracted with a modified Tullgren funnel extractor at a constant temperature of 35 °C in a cabinet for 4 days and collected in ethanol. Measurement of body length and counting were undertaken under a binocular microscope. The specimens of the four species were sorted from the samples, grouped into body length classes and preserved in lactic acid for one week. For each species the number of individuals with gut contents was counted for each body length class. The specimens with visible gut contents could then be selected for the analysis of ingested food.

Although 12 sampling dates were available for the gut contents analysis, only four were used. For each specimen the gut contents were mounted in a small drop of Hoyer's medium on a glass slide and dispersed by lightly pressing the cover slip. Gut contents were examined with a binocular microscope of 400× magnification. Six categories of foods were classified as follows; plant materials (consisting of amorphous mass and plant tissues), fungal hyphae, fungal spores, pollen, mineral particles and animal remains. The area of each food particle was measured using a gridded eyepiece having a total of 100 squares and five replicates (i.e. 500 squares) were examined for each individual. Apart from this, the area of fungal hyphae was estimated by measuring the width and length of each hypha. The percentage of each food was calculated on the basis of their relative areas.

Since 1971, the life cycles and population dynamics of collembolan species have been studied in this study plot. Their species composition and relative abundance are shown in Table 1. These species were classified into two feeding groups according to the form of mouth-parts and observation of gut contents. The species having a well-developed mandibular molar plate are adapted to chew food such as plant and fungal material, while those forms having no molar plate are suctorial and carnivorous (Macnamara 1924). The former feeding groups corresponds to the detritivores identified by Anderson (1978). The latter group constitutes a small part of the collembolan community in terms of species numbers and population density. Amongst the detritivores group, four species were selected for this study on the basis of their abundance.

Table 1. Species composition and mean abundance ($\bar{x}$) of Collembolan species in the study area

Species name	$\bar{x}$ m^{-2}	frequency	feeding type
Hypogastrura sp.	145	0.211	L
Ceratophysella sp.	56	0.082	L
Neanura mandarina Yosii	95	0.138	S
Neanura sanctisebastiani Yosii	27	0.039	S
Anurida sp.	226	0.329	S
Pseudachorutes sp.	145	0.211	S
Xenylla humicola (Fabricius)	29	0.042	L
Friesea mirabilis (Tullb.)	153	0.223	C
Odontella sp.	46	0.067	S
Tullbergia yosii Rusek	16651	24.240	L
Lophognathella choreutes Boerner	17	0.024	L
Onychiurus decemsetosus Yosii	2446	3.561	L
O. sibiricus Stach	220	0.320	L
Tetracanthella sylvatica Yosii	5896	8.583	L
Isotoma sensibilis Tullberg	1264	1.840	L
I. carpenteri Boerner	3098	4.510	L
I. viridis Bourlet	15	0.022	L
Folsomina onychiurina Denis	5392	7.850	L
Folsomia octoculata Handschin	28748	41.851	L
Folsomia candida (Willem)	2	0.003	L
Isotomiella minor (Schaefer)	164	0.239	L
Microisotoma achromata Bellinger	756	1.000	L
Tomocerus varius Folsom	1490	2.169	L
T. punctatus Yosii	2	0.003	L
T. ocreatus Folsom	2	0.003	L
Sinella dubiosa Yosii	363	0.528	L
Homidia socia Denis	17	0.025	L
Homidia sp.	209	0.304	L
Entomobrya sp.	12	0.017	L
Lepidocyrtus sp.	153	0.223	L
Willowsia sp.	2	0.003	L
Oncopodura crassicornis Schoebotham	593	0.863	L
Neelus minutus Folsom	68	0.099	L
Arrhopalites sp.	77	0.112	L
Sminthuridae sp. 1	63	0.091	L
Sminthuridae sp. 2	50	0.051	L
Mean population density of total Collembola	**68692**		

Note: Population density based on the mean of 12 months sampling occasions. Symbols L, S, and C indicate the detritivore, suctorial and carnivore species.

Table 2. The effect of Tullgren extraction on the proportion of individuals with empty guts

Species name	Treatment	Number of individuals	Individuals with gut contents	Individuals with empty guts	
Isotoma carpenteri	flotation	100	79	21	$P < 0.05$
	Tullgren	100	60	40	
Tomocerus varius	flotation	100	38	62	n.s.*)
	Tullgren	100	49	51	
Onychiurus decemsetosus	flotation	100	69	29	$P < 0.05$
	Tullgren	100	53	47	
Folsomia octoculata	flotation	100	71	29	n.s.
	Tullgren	100	67	33	

*) Not significant (n.s.).

3. Results

3.1. Effect of Tullgren treatment on the number of individuals with gut contents

The bias induced by the Tullgren method was examined by comparing the Tullgren samples with those extracted by flotation and the results are shown in Table 2. The effect of treatment was different among the species examined. There was a significant reduction in individuals with gut contents in the cases of *I. carpenteri* and *O. decemsetosus* but no differences in the case of *F. octoculata* and *T. varius*. A likely explanation for the lower proportion of animals with gut contents in the Tullgren samples is that the Collembola voided their gut contents during the extraction process. The extraction was carried out under the same conditions for all samples so the relative amount of loss should remain constant between different sampling dates.

3.2. Seasonal changes in numbers of empty gut individuals

Mean percentages of individuals with empty guts were 37.5, 30.3, 37.2 and 32.3 for *F. octoculata*, *O. decemsetosus*, *T. varius* and *I. carpenteri* respectively. Seasonal changes in the proportion of empty gut individuals in populations are shown in Fig. 2 and were different among the species examined. *T. varius* showed no clear seasonal variations in the proportion of empty gut individuals. Seasonal variations in the empty gut individuals of *I. carpenteri* and *F. octoculata* showed a similar pattern and had a peak in February and March. In the case of *O. decemsetosus*, there were two peaks in numbers of individuals with empty guts. To examine the factors affecting the seasonal changes in numbers of empty gut individuals, rank correlation coefficients between the proportion of empty gut individuals and soil temperature and soil water contents were calculated for the four species (SIEGEL 1958). The coefficient was significant for two combinations i.e. *I. carpenteri*×soil temperature and *F. octoculata*×soil temperature.

3.3. Analysis of gut contents

Mean percentages of food items in gut contents of the four species are shown in Table 3. In every species, gut contents consisted largely of plant and fungal materials and the other components constituted a minor proportion of their food.

Seasonal variations in percentages of plant matter, fungal hyphae and spores are shown in Fig. 3. Seasonal variations of fungal hyphae and plant matter were statistically examined by using ANOVA. The variations of plant matter were significant for *T. varius* ($F = 11.04$, $P < 0.01$), and *I. carpenteri* ($F = 3.56$, $P < 0.05$) but were not significant for *F. octoculata* ($F = 1.38$, n.s.) and *O. decemsetosus* ($F = 4.67$, n.s.). The variations of fungal hyphae were significant for *T. varius* ($F = 7.24$, $P < 0.01$) and *I. carpenteri* ($F = 19.2$, $P < 0.01$) but were not significant for *F. octoculata* and *O. decemsetosus*. Seasonal variations in the proportion of fungal hyphae and plant matter in gut contents were compared among the four species by using Kendall's concordance and the coefficient was significant at $P < 0.01$ probability of error. The four species of Collembola showed a similar seasonal variation in gut contents and animals had a tendency to take more fungal hyphae during autumn and winter than summer and spring.

Table 3. Composition*) of the gut contents of four species of Collembola

Food source	*T. varius*	*I. carpenteri*	*F. octoculata*	*O. decemsetosus*
Plant detritus	*74.52*	*80.90*	*86.29*	*73.80*
Fungal hyphae	*19.40*	*15.84*	*11.39*	*22.94*
Pollen	*1.14*	*1.17*	*1.12*	*0.11*
Spores	*3.04*	*1.47*	*0.77*	*2.39*
Mineral particles	*0.44*	*0.49*	*0.38*	*0.47*
Algae	*0.91*	*0.13*	*0.07*	*0.30*
Animal remains	*0.55*	0	0	0
Number of individuals examined	182	173	152	123

*) Relative proportions of components.

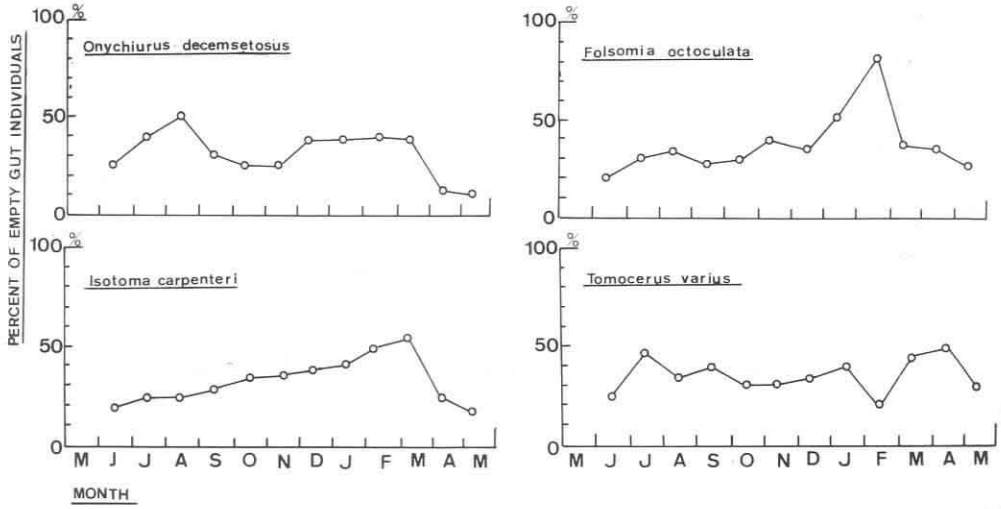

Fig. 2. Seasonal changes in numbers of individuals with empty guts.

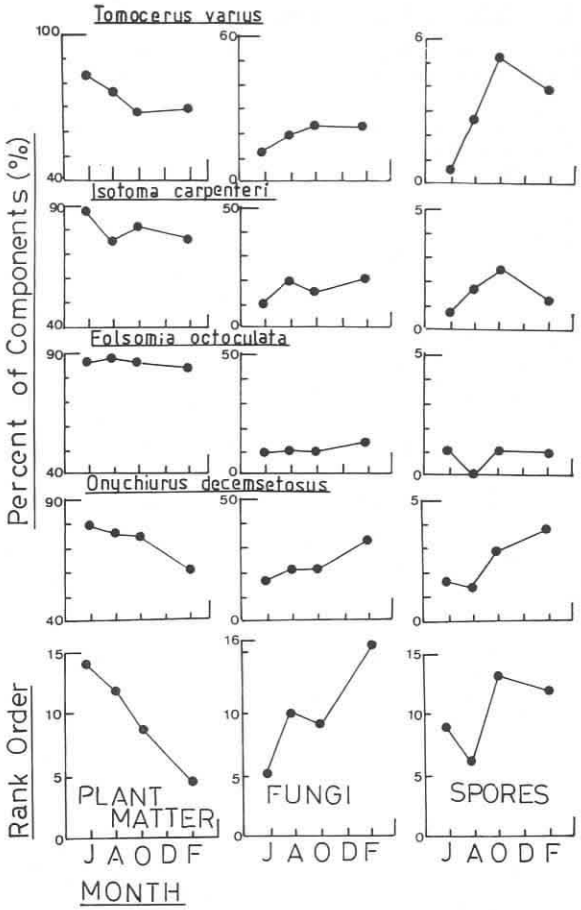

Fig. 3. Seasonal changes in the major food items of four species of Collembola and rank order of the major food items.

Table 4. Comparison of the gut contents*) between different size classes of Collembola

Size class	*Isotoma carpenteri*			*Tomocerus varius*		
	Plant detritus	Fungi	Spores	Plant detritus	Fungi	Spores
1st ($\leq$ 0.375 mm)	79.49	17.98	1.35	80.08	17.70	1.54
2nd (0.375—0.500 mm)	82.55	14.71	1.73	78.87	16.10	1.60
3rd (0.500—0.625 mm)	79.99	16.74	1.89	75.63	18.63	4.05
4th (0.625—0.750 mm)	79.20	16.16	1.31	68.90	23.86	5.29
5th ($\leq$ 0.750 mm)	86.55	10.66	0.50	69.51	20.50	2.18
Size class	*Folsomia octoculata*			*Onychiurus decemsetosus*		
	Plant detritus	Fungi	Spores	Plant detritus	Fungi	Spores
1st	92.12	6.67	0.17	80.91	18.01	1.04
2nd	86.83	12.24	0.39	81.91	17.30	0.80
3rd	85.73	11.51	0.36	71.67	25.19	2.70
4th	79.78	15.52	2.38	58.49	33.13	5.77

*) Relative proportion of components.

In this study, animals collected were separated into body length classes which closely correspond to age of individuals (GRÉGOIRE-WIBO 1973 and NIIJIMA 1973). Gut contents were compared between different size classes and showed that older animals had a tendency to take more fungal hyphae (Table 4).

Food contents between the four species were examined using the niche overlap index proposed by PIANKA (1974). The values of overlapping of food items were calculated by the following formula:

$$\alpha_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

where p_{ij} and p_{ik} present the proportion of the i food items used by the j and k species. A value of 1.00 indicates a complete overlap of food items. The values were calculated for the 6 combinations of species and ranged between 0.968 and 0.999 (Table 5).

Table 5. Indices of food niche overlapping between four Collembola species*)

	T. varius	*I. carpenteri*	*F. octoculata*	*O. decemsetosus*
T. varius	—	0.996	0.989	0.969
I. carpenteri	0.996	—	0.999	0.986
F. octoculata	0.989	0.999	—	0.985
O. decemsetosus	0.969	0.976	0.985	—

*) The formula for calculation of the overlap index by PIANKA (1974) is given in section 3.

The results indicate that the overlapping of food items between species was very high in every combination of species and suggest that the four species have the same food preference.

4. Discussion

Collembolan species may be divided into two feeding groups, i.e. suctorial and detritivore groups on the basis of mouth-part morphology. The collembolan community in this study area consisted of 36 species, 31 detritivores and 5 suctorial. The detritivore species were dominant in the collembolan community in terms of population abundance and spe-

Table 6. Results of gut content analysis*) for collembolan species from various localities

Species name	Plant detritus	Fungi	Pollen	Animal matter	Minerals	Rest	References
Hypogastrura tullbergi	71.3	11.7	0	8.5	8.4	0	Addison & Parkinson (1978)
	86.8	8.2	0	0	0	0	
Folsomia regularis	83.4	4.0	0	0	12.6	0	Addison & Parkinson (1978)
Onychiurus furcifer	81.3	12.7	0.7	2.3	3.0	2.5	McMillan & Healey (1971)
O. armatus	81.3	18.2	0.3	0.1	0.1	0.5	McMillan & Healey (1971)
O. variabilis	70.0	27.1	0.3	1.8	0.1	1.5	McMillan & Healey (1971)
Tullbergia callipygos	93.9	5.9	0.1	0	0.1	1.5	McMillan & Healey (1971)
Lepidocyrtus lignorum	27.2	72.7	0.1	0	0	1.0	McMillan & Healey (1971)
Tomocerus minor	68.9	30.3	0.5	0.2	0	0.3	McMillan & Healey (1971)
T. flavescens	52.6	46.8	0.4	0	0.2	0.3	McMillan & Healey (1971)
Bourletiella hortensis	44.8	3.0	5.5	0	45.0	1.7	Marshall (1978)
Tomocerus ocreatus	75.8	24.2	0	0	0	0	Takeda (1972)
T. kinoshitai	90.5	9.5	0	0	0	0	Takeda (1972)
Tomocerus varius	74.5	22.4	1.1	0.5	0.4	1.1	present results
Isotoma carpenteri	80.9	17.3	1.1	0	0.5	0.2	present results
Folsomia octoculata	86.3	12.1	1.1	0	0.4	0.1	present results
Onychiurus decemsetosus	73.8	25.3	0.1	0	0.5	0.3	present results

*) Relative proportion of components.

cies numbers which seems to be a common feature in soil collembolan communities. The detritivore species may occupy a different food niche from that of suctorial species in a habitat.

The feeding biology of Collembola has been studied mainly for the detritivore species. Feeding preference of the detritivore species has been studied by analysing the gut contents of field populations and the results of gut contents' analysis from various localities are summarized in Table 6 together with the present results. In this study area, the four detritivore species showed a very similar appearance in gut contents and the relative abundances of the gut constituents appeared to be similar to those of available foods in this habitat. The present results together with the previous studies suggest that detritivore species are unspecialized and indiscriminate feeders.

Current competition theory suggests that animals living together in a habitat show a reduced competition by occupying different food niches. The view may be applicable to the two feeding groups of Collembola, but the detritivore species of Collembola in this habitat coexist without apparent segregation of food niches. Anderson & Healey (1972) have noticed the apparent ability of large numbers of detritivore species to coexist in a habitat while utilizing identical or very similar food resources. They have proposed the following four hypotheses to explain this ability for coexistence: (1) the availability of excess food for Collembola, (2) differences in their utilization of food resources such as coprophagy, (3) microhabitat differences between species.

In this study plot, the A_0 layer is about 3—4 cm in depth and there is a high accumulation of organic matter which seems to be a common feature of forest soils in temperate forests (Tsutsumi 1973). Therefore there may be an excess of food for Collembola.

Soil is generally heterogeneous in composition as shown by the horizontal and vertical heterogeneity of accumulation of organic matter. In this study plot, the four species showed a habitat preference within the organic soil layers. Collembola species showed an aggregative distribution in this study plot and the degree of aggregation was specific according to the response of individuals to habitat conditions (TAKEDA 1978, 1979b). Soil Collembola are not as free from environmental conditions as other free-living terrestrial insects which have developed a resistance to desiccation in terrestrial life. The aggregative distribution and vertical distribution of the four species of Collembola suggest that they may be restrained by some environmental conditions such as soil water. The environmental restraint may be related to the microhabitat utilization of collembolan species.

High percentages of individuals with empty guts were observed in this study and have been reported by some workers (ANDERSON & HEALEY 1972, JOOSSE & TESTERINK 1977 and ADDISON & PARKINSON 1978). CHRISTIANSEN (1961) suggested that Collembola with empty guts may be feeding on bacteria which would not be visible in normal gut content preparations. This explanation may be true for the suctorial feeding group which usually take fluid materials, but seems to be unreliable for the chewing type species. The empty gut reflects rather the feeding condition of individuals and the seasonal changes in proportion of individuals with empty guts in the populations would represent the feeding activities of collembolan populations. The empty gut individuals in populations have been attributed to the operation of the moulting cycle of collembolan species (JOOSSE & TESTERINK 1977). Species such as *Tetracanthella sylvatica* [TAKEDA 1976] and *Subisotoma variabilis portucalensis* [POINSOT 1971] having a diapause or an aestivation period in their life cycle, show an arrest of feeding during the non-active periods. TESTERINK (1981) has shown that an *Orchesella cincta* population stopped feeding in dry conditions. In this study the proportion of empty gut individuals in a population showed seasonal variations and the feeding activities of *F. octoculata* and *I. carpenteri* were positively correlated with soil temperature. The feeding activity of *T. varius* was dependent upon environmental conditions and *O. decemsetosus* showed two peaks in the proportion of empty gut individuals. The reduction of feeding individuals in populations at this site may therefore be related to the high temperature or drought conditions in summer and to low temperature in winter. These seasonal changes in feeding activities were specific according to the response of individuals to environmental conditions and may contribute to the reduction of competition for food.

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Seasonal changes in feeding activities and gut contents of four species of Collembola were studied in a pine forest during one year. The feeding activity of *Folsomia octoculata* and *Isotoma carpenteri* were correlated to the soil temperature and were decreased during the autumn and winter periods. For the other species, there was no correlation between the feeding activity and environmental factors.

Seasonal variations in gut contents were significant for *Isotoma carpenteri*, *Tomocerus varius* and *Onychiurus decemsetosus* in which fungal materials increased inversely to plant materials during the winter period. Seasonal variations of fungal and plant materials showed a similar pattern for the four species and animals had a tendency to take more fungal materials during autumn and winter.

Gut contents of four species were compared using the niche overlap index and there were no marked differences in gut contents of the four species. Gut contents of different-sized individuals were compared and the results showed that the adults had a tendency to take more fungal material than did the juvenile individuals.

Key words: Collembola, Insecta, Apterygota, food, feeding activity, gut content, and seasonal variation.